A STUDY OF THE RESPONSE OF OYSTERS TO TEMPERATURE, AND SOME LONG RANGE ECOLOGICAL INTERPRETATIONS[1]

by

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Introduction

PHYSIOLOGICAL EFFECTS OF TEMPERATURE[2]

The Pumping Rate of Oysters in Relation to Water Temperature

Much has been written on the response of oysters to temperature, but in respect to long term observations the experimental work on this subject has been limited. During the period from December, 1946, to July, 1950, the author had an unusual opportunity to study the detailed behavior of the oyster, *Crassostrea virginica* (Gmelin), in the laboratory as well as in the field. This paper will present the results of some of the studies on rates of filtration as related to temperature. These results will then be interpreted in the light of recent and paleoclimatology of the Gulf of Mexico area.

The discussion to be given here is based on the continuous recording of the shell movement and pumping rate of 66 oysters. The record for any given individual ranged from three weeks to six months, with minor interruptions. Some of the oysters made significant growth during the period of recording. Temperature observations were made with precision thermometers at intervals of four to eight hours. The sea water was pumped directly from the bay by a high pressure, high velocity system, without intermediate storage.

Involved in this analysis were 64,580 record hours, for each of which the effluent of the oysters has been computed, and the water temperature at that hour determined. Because of the comparatively long intervals (four to twelve hours) at which the temperature observations were made, we cannot indicate all of the hourly temperatures as observed, but only as interpolated values. Because of this, the data are presented in terms of temperature intervals of 5° C.

[1] The experimental work which forms the basis for this paper was performed by the author while he was engaged in investigations supported by private resources. The conclusions and interpretations do not necessarily represent the views of the present employer of the author.

[2] Acknowledgments: I wish to extend my appreciation to Messers. Sammy M. Ray, A. W. Magnitzky, and Joe O. Bell for their attentive and diligent assistance in the laborious field and laboratory exercises which produced the large body of data referred to in the following pages.

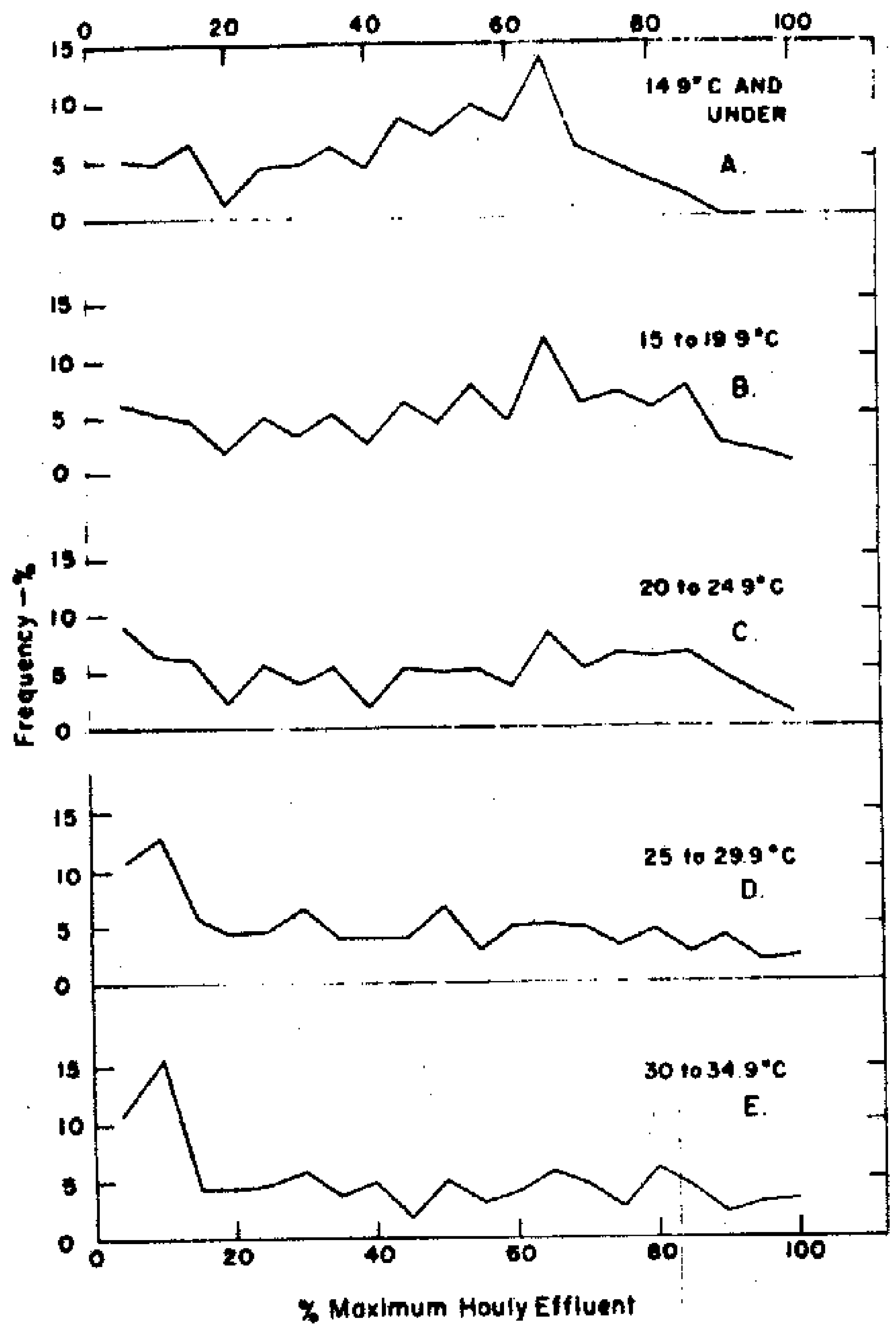


Figure 1. Frequency distribution of hourly effluents (in terms of percent of maximum hourly effluent for a given oyster) for the various temperature brackets. See text for full explanation.

TABLE I.

	Temperature intervals, °C.	Number of Oysters	Number of hours recorded
A.	14.9 and under	30	3,257
B.	15 to 19.9	37	23,964
C.	20 to 24.9	48	14,459
D.	25 to 29.9	39	19,138
E.	30 to 34.9	19	3,762
			64,580

Table I gives the temperature intervals into which the pumping rates were classified and the number of recorded observations in each. The number of oysters in the several intervals totals more than the 66 oysters used because of the overlapping of many of the specimens from interval to interval.

The hourly effluents for each oyster were converted to per cent maximum hourly effluents in order to permit a combination of all data for treatment. For instance, a small oyster pumping 10 liters per hour with a maximum of 12 liters per hour could not be compared with a large oyster pumping 10 liters per hour but with a possible maximum of 30 liters per hour. Frequency distributions of hourly effluents determined on this basis were then computed f the five temperature brackets shown in Table I, and the results are plotted Figure 1.

In Figure 1 it is clear that as the intervals of higher temperatures we entered there was a tendency for the maximum pumping rate to increase up to interval C. In temperature interval A there is a definite mode at approximately the 60% level; in B, at about the 75% level with more spread towards higher rates. In interval C, the mode has advanced to about the 80% level with a tendency to build up the higher levels. In D and E the trend is reversed and the very low percentages are increased.

Figure 2 demonstrates the relationship between the hours of closure an temperature. As would be expected from the foregoing, the hours of closure increase with increasing temperatures.

Loosanoff (1950) noted the following relationships between pumping rate and temperatures: 8° to 16° C., increasing; 16° to 28° C., no fluctuations 28.1° to 32° C., a further increase; 32.1° to 34° C., rapid; 34° and over, dis tress. He further stated that oysters which had been held at 3° to 5° C. an suddenly transferred to water of about 20° C. quickly increased their pumpin rate to that of control oysters held at 20° C. No experimental data were given with these results and it is not known at what time of the year these experiments were performed, how many oysters were used, nor how long they were subjected to the experimental temperatures. In view of our results, th inference of Loosanoff's note is that his oysters responded as might be expected when temperature is the only variable. In fact, his results paralle those of Gray (1928) on the response of ciliary beat in mytilus to tempera-

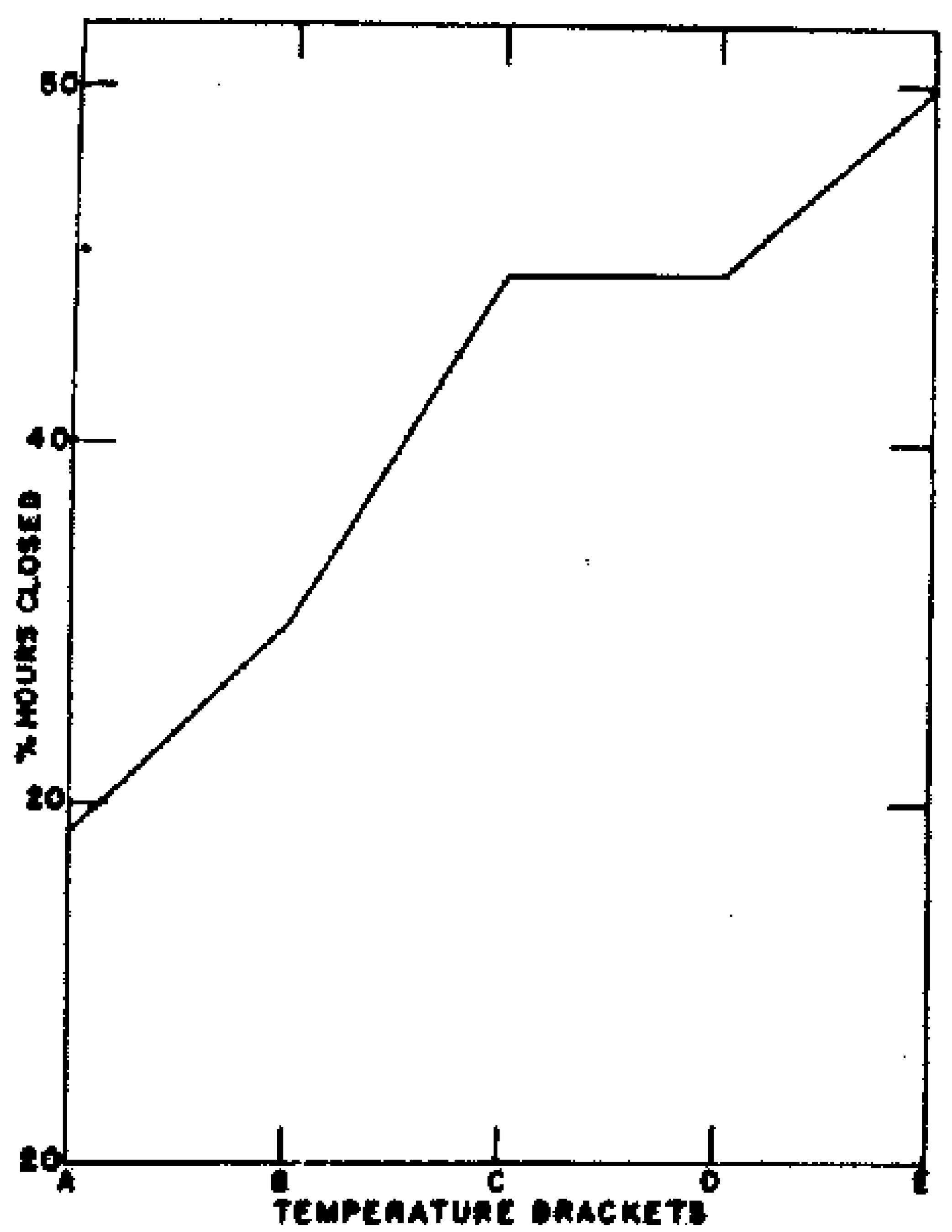


Figure 2. Closure time (percent of record hours) for all oysters at the various temperature levels. Total record hours involved at each level given in Table 1. Temperature brackets are also indicated in Table 1.

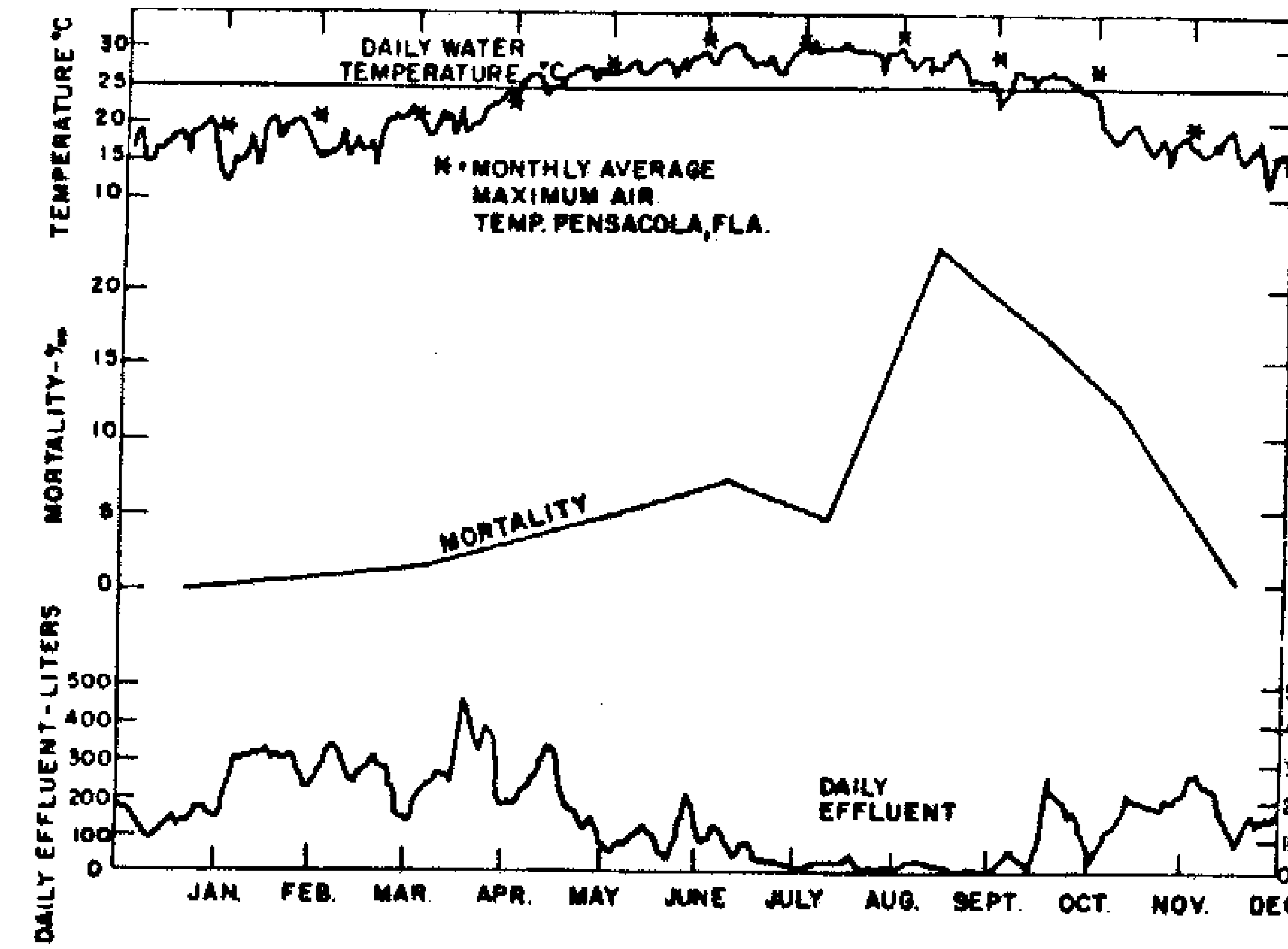


Figure 3. A simultaneous indication of daily water temperatures, mean monthly maximum air temperatures (Pensacola, Florida), monthly oyster mortality in percent, and mean daily effluent of experimental oysters in liters. The daily water temperatures were taken from a thermograph situated in Santa Rosa Sound near the laboratory, and the air temperatures were derived from the records of the Pensacola station of the U. S. Weather Bureau. The oyster mortality curve represents data from oysters held in rafts near the laboratory. The daily effluents of the oysters were computed from the same set of data summarized in Table 1.

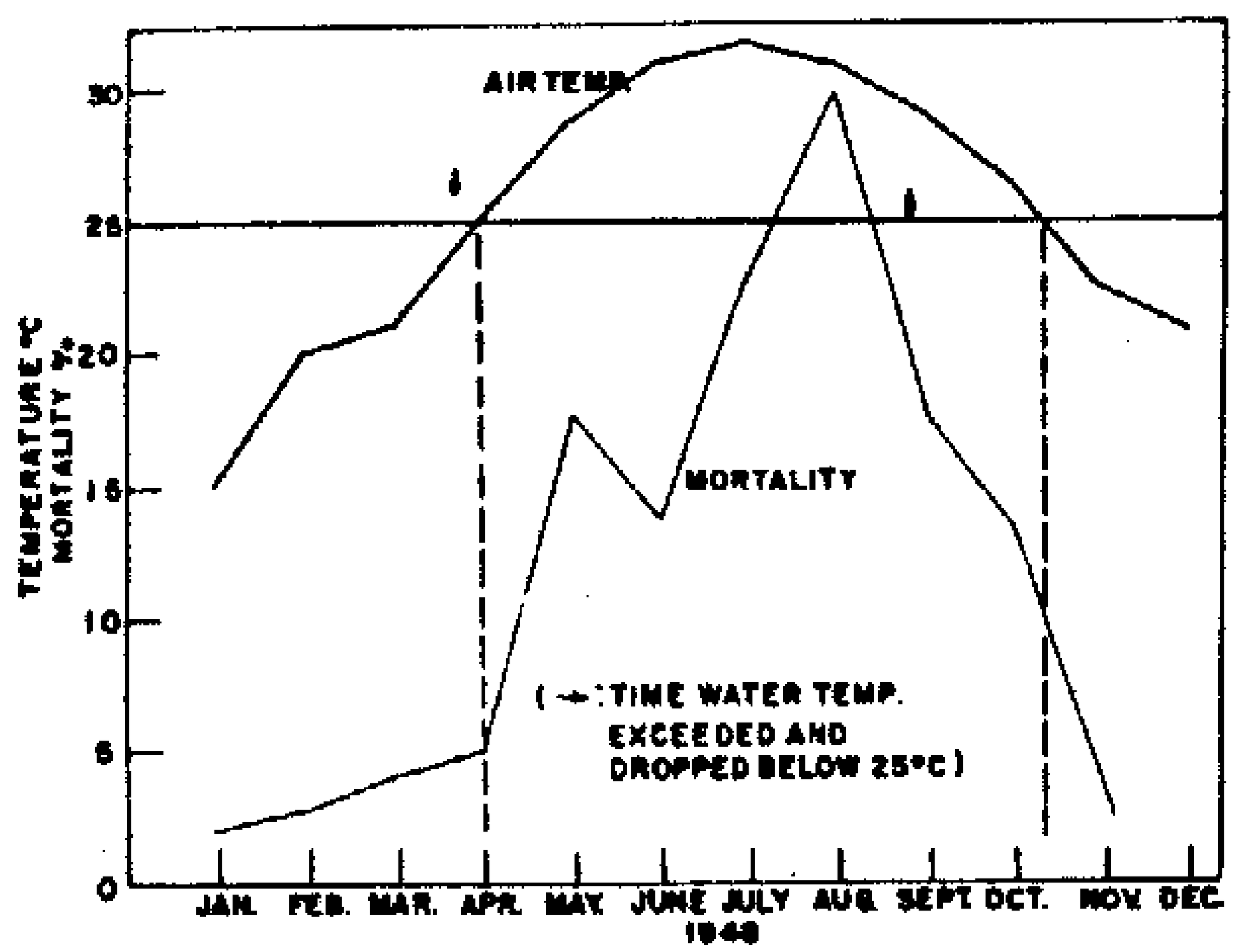


Figure 4. This figure summarized data collected in Grand Bay, Plaquemine Parish, Louisiana. The mortality curve was obtained from a set of oysters retained in tanks as explained in the text. The mean monthly maximum air temperature would show closer agreement with the water temperatures if the water temperatures were shown as monthly means as are the air temperatures.

ture. Gray shows that the cilia increase their activity with increasing temperature up to 28° C., and that beyond this the ciliated epithelium tends to disintegrate.

In an earlier report (Collier et al, 1950) it has been shown that there is a chemical factor which has an important influence on the pumping rates of oysters. This factor is what we call at present the "carbohydrates" or "N-ethyl-carbazol substances". It has been shown that these substances are required in increasing amounts as temperatures rise. Even at low temperatures the oyster seems to pump faster when these naturally occurring substances are present in greater quantity, but the absolute thresholds are lower. At higher temperatures the threshold value for minimum pumping is higher, and even greater quantities are required for maximum pumping. It would seem then, that the ciliated epithelium of the oysters' gills follows in general the equation of Arrhenius, provided there are sufficient quantities of some natural carbohydrate materials present in the water.

In view of the evidence given above, the optimum temperature range for the filtration of water by Gulf Coast oysters is approximately 15° to 25° C.

Temperature, Pumping and Mortality

In a series of raft experiments which were in progress near the laboratory at which the above temperature and pumping rate data were collected, mortality records were kept on a group of oysters during the same period of time. In Figure 3 the elements of daily effluent (mean daily effluent of all oysters), bi-weekly mortalities in percent, and temperature have been plotted. The mortality figures are based on a total of 1200 oysters. These were divided into sub groups held under a variety of conditions, but all groups followed the trend shown here. It is not difficult to see that high temperature, low pumping rates, and mortalities were coincident. During this period the growth rates were sharply depressed from June through September (unpublished data). This is in agreement with some temperature studies made in Long Island Sound (Loosanoff and Nomejko, 1949). In that case, a significant decline in rate of increase of shell length and shell width occurred in going from 20° to 25° C. In their discussion of the matter Loosanoff and Nomejko say, "Thus, under the conditions under which the experiment was run, the oysters grew most rapidly at temperatures of 15.0° and 20.0° C. Therefore the optimum range for their growth was either confined between these two temperatures or, what is more probable, extended a degree or two outside these two limits, giving a range from approximately 13.0° to 22.0° C." These authors did not give these values as final, but it is significant that we should be so nearly able to confirm them even in the waters of the Gulf of Mexico.

During 1948 another set of data were collected at Grand Bay, Louisiana, by the daily observation of 144 oysters held in tanks with water circulated over them. The water was pumped into the tanks constantly at a mean rate of 700 liters per hour in each tank with waste going overboard. Figure 4 shows the relation between this mortality and the average monthly maximum air temperatures at Burrwood, Louisiana. Here again, we find a close association

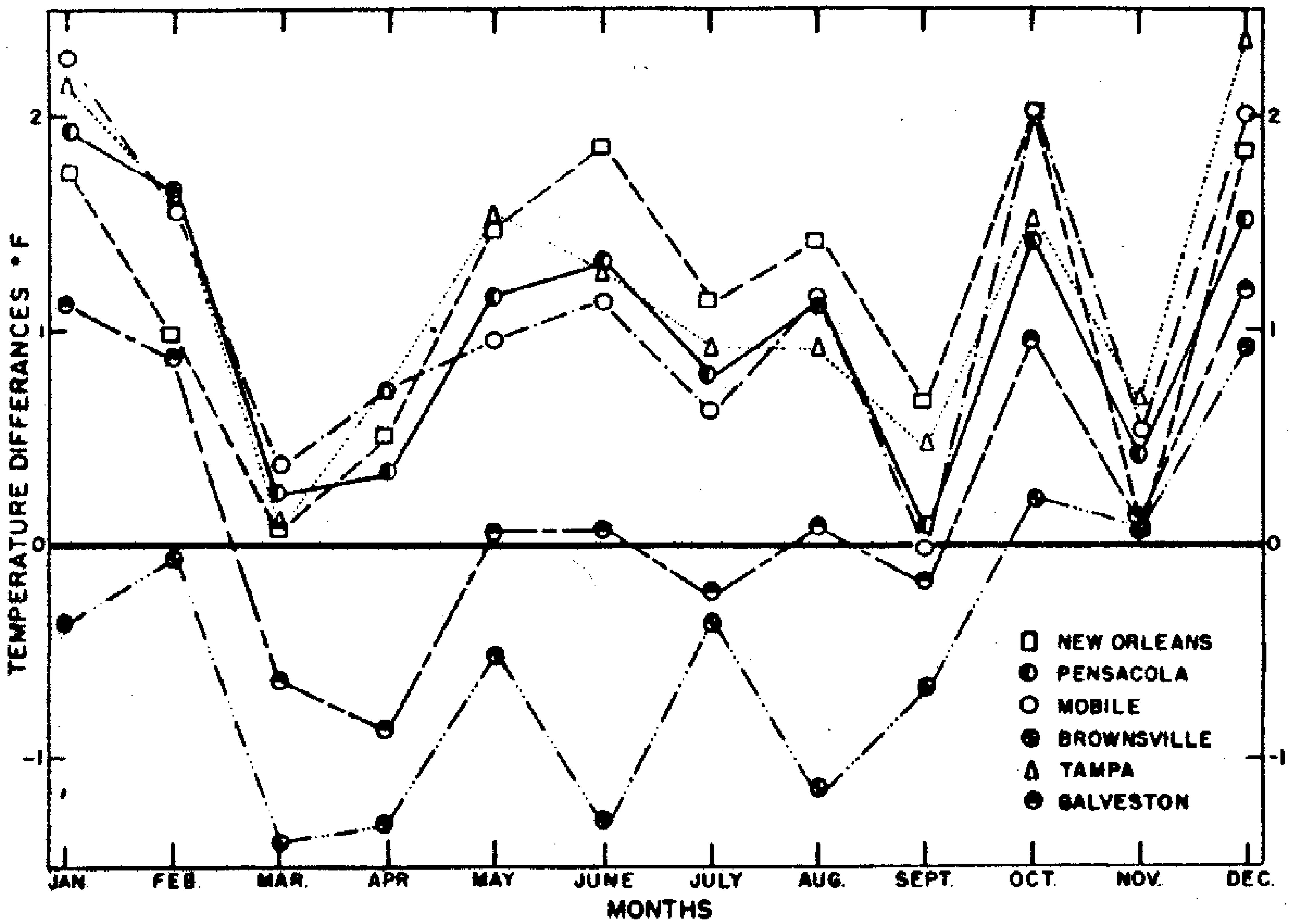


Figure 5. Differences in mean monthly maximum temperatures between the period of record preceding and including 1930, and the period 1931-1952. For actual values and statistical significance see Tables II through VII. See text for discussion.

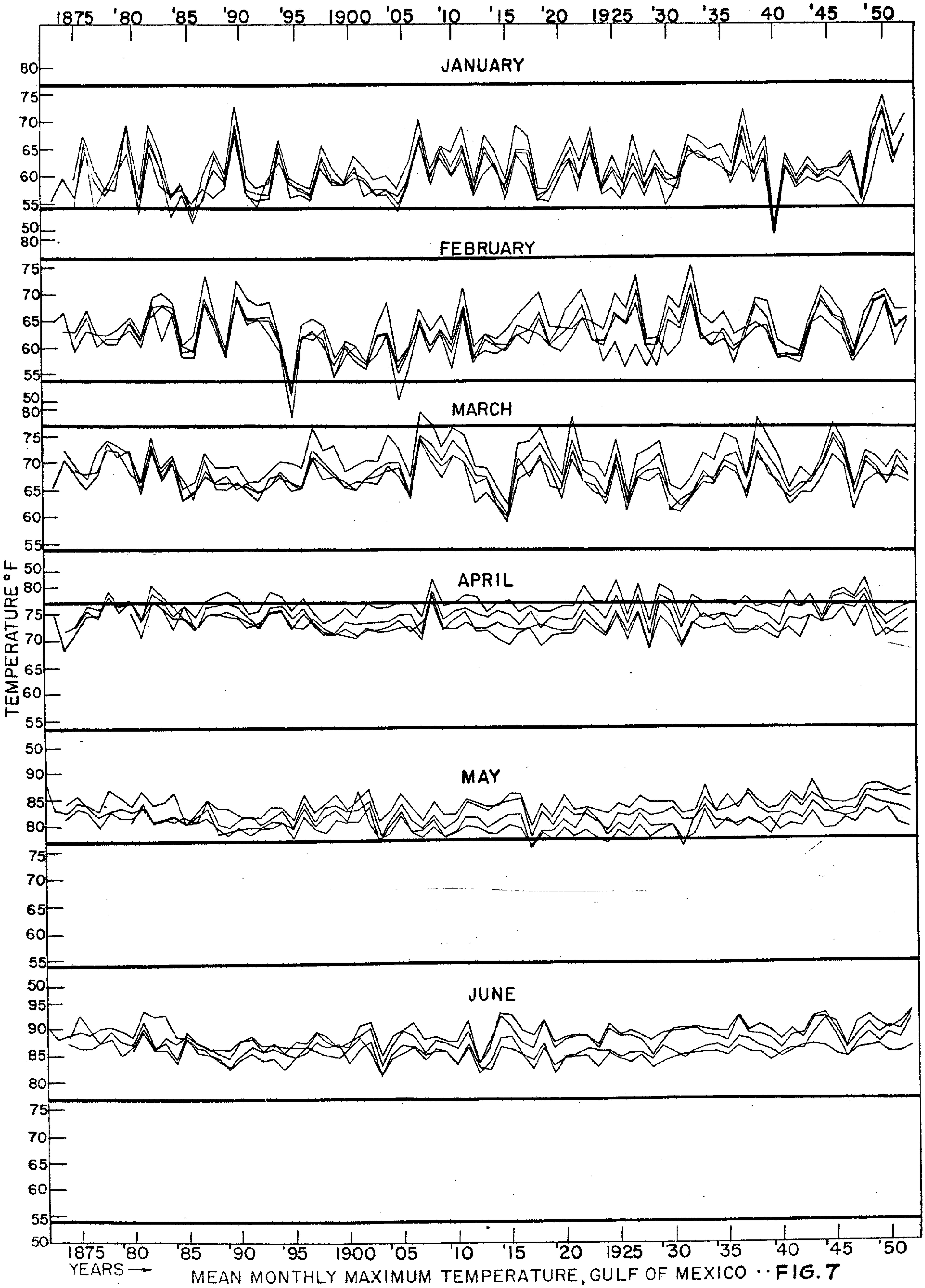
The most outstanding characteristic is the negative difference shown at Brownsville (i.e., a tendency for the maximum temperatures to be lower), with little change for Galveston during the summer, and the large positive differences for the remainder of the points. This would make it seem that Galveston is a point at which the forces causing the changes are in balance and, in effect, provide a fulcrum for dropping maxima to the southwest and rising maxima to the east.

As shown in Figure 5 the month-to-month trend is similar at all points and from this we can conclude the general trend for the northeastern Gulf is definitely upward for all months of the year except March, September and November. Even Brownsville, shows a tendency to increase in December. There are some points, Galveston for January, for instance, whose increase would be significant according to the student t test (Table V) because of the erratic climate brought about by the northers so characteristic of the Gulf Coast. However, when these increases are in agreement with the trends at other points which are themselves significant it seems likely that the Galveston increases are significant, but with the element of mathematical probability obscured by the "northers".

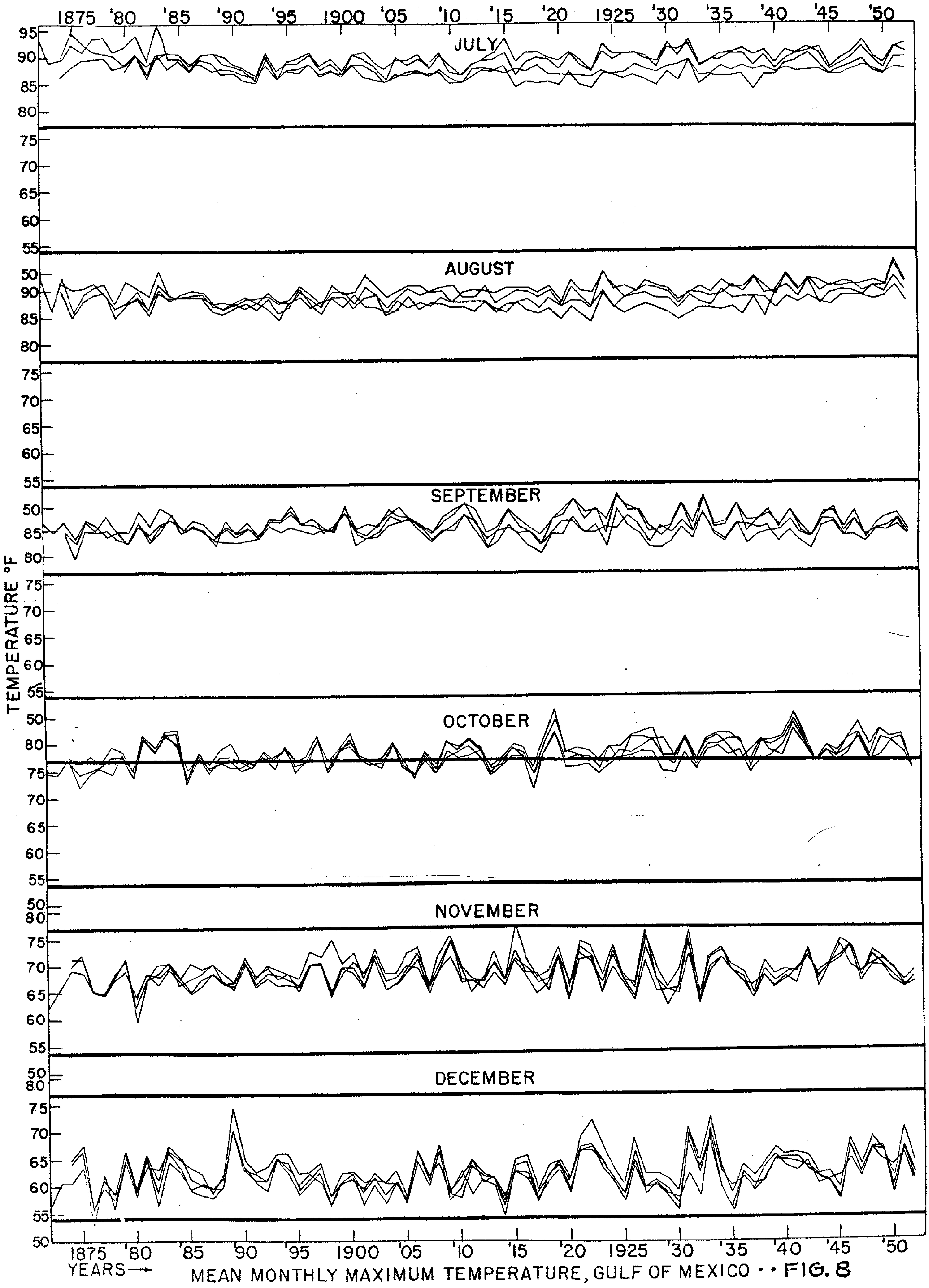
Mitchell (1953) has correlated some portion of such secular climatic changes as we are pointing out with the growth of cities. His treatment is based on mean temperatures rather than mean maxima, and he has divided the United States into six rather broad regions. The one considered in this paper is split, in his work, into two regions (Zones V and VI), and Brownsville are omitted altogether from his considerations. The Gulf maritime province would have to be isolated for special study by a treatment such as Mitchell's before the effect of increasing population of Gulf Coast cities could be evaluated. For these reasons it is not possible to compare the results of Mitchell's investigation with those presented here.

Although it is possible that changes indicated here might be slightly aberrant because of industrial influences, it should be remembered that at the time that some of the largest changes are shown the winds are largely from over the Gulf of Mexico. In some cases the cities which have shown a significant increase in mean monthly maxima have had only moderate industrial or population growth - Pensacola, for example. For the purpose of this discussion we are justified in the examination of the climatic record on the basis of average monthly maxima.

If the 77° F. line is taken as zero, and the years are divided into two 35 year periods (1882 to 1916, both inclusive, and 1917 to 1951, both inclusive) and the temperature deviations around the zero are summed algebraically we will find that the results are as shown in Table VIII. It would certainly seem from this that summer temperatures are being extended into the fall months. This is probably to be expected if we follow Charlesworth (1953) the following statement: "Today the glaciers of the world are in retreat, though not always with the same intensity or without sporadic spurts of short duration and small amount. This universal wasting is affecting the glaciers from the Artic to the Antartic, including those of the tropics. It set in



MEAN MONTHLY MAXIMUM TEMPERATURE, GULF OF MEXICO ·· **FIG. 7**



MEAN MONTHLY MAXIMUM TEMPERATURE, GULF OF MEXICO · · FIG. 8

the Gulf of Mexico. This cool water fauna is interpreted as late glacial and has features characteristic of the continental slope water between Cape Hatteras and Cape Cod in the western North Atlantic." This is evidence from another approach that lower water temperatures than those presently observed prevailed in the Gulf of Mexico at the time of the earliest known appearance of Crassostrea virginica. Hilgard (1878) reported the presence of specimens of Urosalpinx cinereus in sub-surface strata in the Mississippi River delta which are probably of the same age as the earliest formations in which Crassostrea virginica appears. As far as we know, Urosalpinx has long since disappeared from the Gulf of Mexico.

It is possible that if the climate continues its present trend Crassostrea virginica will decline as a community dominant. This will depend on whether or not there exists in this species the genetic potential to produce a race which can survive the high temperatures.

SUMMARY AND CONCLUSIONS

1. A combined study of pumping rates, growth rates, and mortality rates show that the optimum temperature range for Crassostrea virginica lies between 15° and 25° C., even on the Gulf Coast. The poleward limit for this species is determined by the minimum spawning temperature of approximately 16° C., and the equatorward limit is determined by the maximum temperature favoring survival, which we consider to be 25° C. This type of distribution fits Hutchin's (1947) group 3.

2. It is shown that in general, water temperatures for estuaries bordering the Gulf of Mexico can be inferred from average monthly maximum air temperatures.

3. The northern Gulf estuarial waters are within these temperature limits for approximately five months out of the year, but Weather Bureau records show a definite increase in the average monthly maxima of the last 22 years. September is already above the maximum, and since 1916 the average maxima for October have gone above 25° C.

4. Evidence that the Gulf waters were cool at the earliest known time Crassostrea virginica is recorded in the Gulf can be found in the works of the paleontologist and the paleoclimatologist. They were comparable to present day waters between Cape Hatteras and Cape Cod.

5. It is pointed out that although oysters can survive as individuals in the southern reaches of the U. S. Gulf Coast, it has been only on the north Gulf that they have survived as community dominants. This is in agreement with the above statement concerning the optimum temperature range and the temperature zones of the Gulf.

6. It is concluded that since Crassostrea virginica appears to be fundamentally a cool water animal, and since the waters have been becoming continuously warmer, particularly in the last thirty years, its position as a community dominant in the north Gulf is threatened if the warming continues.

7. There are other factors affecting the survival of oysters including Dermocystidium infestation, predators, changing salinities, silting, floods, river levees, and overfishing. Low water temperatures assist the animal to resist all of these except the last. Of these, the most important on the Gulf Coast at this time is probably Dermocystidium, but the attacks of this organism are predicated on the debilitation brought about by prolonged exposures to excessive heat. There is evidence that the presence of some natural carbohydrate substances in the sea water assist the oyster to filter water in spite of temperatures above 25° C.

8. The future of the Gulf oyster industry is not very bright. Cultch spreading activities and seed planting are probably helpful for brief periods, but are too expensive in view of the uncertain returns. The perfection of a heat resistant stock of oysters by husbandry offers some possibility, but the limited success of the species in maintaining itself in lower Gulf waters is not encouraging.

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TABLE II

Tampa

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" _t_ test.

			A			B		
			Beginning of record through 1930			1931 – 1952 (both inclusive)		
Month	Difference of means (B – A)	t A:B	n	s	$\bar{x}$	$\bar{x}$	s	n
Jan.	+ 2.153	2.1149*	40	3.287	69.688	71.841	4.686	22
Feb.	+ 1.610	1.5203	40	3.633	71.135	72.745	4.579	22
March	+ 0.081	0.0831	40	3.573	76.133	76.214	3.851	22
April	+ 0.744	1.3025	41	2.205	80.415	81.159	2.076	22
May	+ 1.514	3.6981**	41	1.532	85.422	86.936	1.580	22
June	+ 1.273	3.4791**	41	1.286	88.559	89.832	1.555	22
July	+ 0.917	2.9628**	41	1.010	89.183	90.100	1.427	22
Aug.	+ 0.916	3.1019**	41	1.094	89.507	90.423	1.160	22
Sept.	+ 0.475	1.4226	41	1.275	88.207	88.682	1.241	22
Oct.	+ 1.523	2.9362**	41	2.027	82.415	83.938	1.730	22
Nov.	+ 0.658	1.0322	41	2.232	75.861	76.519	2.640	22
Dec.	+ 2.384	2.8220**	41	2.746	70.368	72.752	3.827	22

* Significant at .05 level ** Significant at .01 level

TABLE III

Pensacola

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" _t_ test.

			A			B		
			Beginning of record through 1930			1931 – 1952 (both inclusive)		
Month	Difference of means (B – A)	t A:B	n	s	$\bar{x}$	$\bar{x}$	s	n
Jan.	+ 1.937	1.9415	51	3.5995	60.063	62.000	4.5692	22
Feb.	+ 1.667	1.7728	51	3.6355	61.710	63.377	3.8064	22
March	+ 0.247	0.3091	51	3.1149	67.180	67.427	3.1714	22
April	+ 0.343	0.6556	51	1.9760	73.125	73.468	2.2195	22
May	+ 1.151	2.2569*	51	1.9951	79.767	80.918	2.0095	22
June	+ 1.335	2.7146**	51	1.8355	85.233	86.568	2.1322	22
July	+ 0.790	1.9706	51	1.5066	86.765	87.555	1.7163	22
Aug.	+ 1.113	2.6645**	51	1.3482	86.996	88.109	2.1769	22
Sept.	+ 0.064	0.0141	51	1.8658	84.641	84.705	1.5469	22
Oct.	+ 1.421	2.4856*	51	2.2436	76.984	78.405	2.2351	22
Nov.	+ 0.413	0.6688	51	2.2762	67.792	68.205	2.7346	22
Dec.	+ 1.502	1.8665	51	2.9570	61.425	62.927	3.5818	22

* Significant at .05 level ** Significant at .01 level

TABLE IV

Mobile

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" t test.

			A			B		
			Beginning of record through 1930			1931 - 1952 (both inclusive)		
Month	Difference of means (B - A)	$t_{A:B}$	n	s	x̄	x̄	s	n
Jan.	+ 2.280	2.1526*	58	4.016	59.743	62.023	4.763	22
Feb.	+ 1.522	1.6009	58	3.813	62.528	64.050	3.753	22
March	+ 0.374	0.4339	58	3.455	68.376	68.750	3.407	22
April	+ 0.745	1.3400	58	2.328	74.964	75.709	1.897	22
May	+ 0.964	1.8436	59	2.217	82.281	83.245	1.706	22
June	+ 1.142	2.2322*	59	2.145	88.081	89.223	1.751	22
July	+ 0.631	1.1640	59	2.364	89.369	90.000	1.511	22
Aug.	+ 1.169	2.8360**	59	1.672	89.217	90.386	1.587	22
Sept.	- 0.012	0.0241	59	1.961	86.207	86.195	2.092	22
Oct.	+ 2.026	3.2746**	59	2.511	77.469	79.495	2.380	22
Nov.	+ 0.543	0.8396	59	2.525	67.934	68.477	2.757	22
Dec.	+ 2.044	2.3699*	59	3.363	60.820	62.864	3.689	22

* Significant at .05 level ** Significant at .01 level

TABLE V

New Orleans

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" t test.

			A			B		
			Beginning of record through 1930			1931 - 1952 (both inclusive)		
Month	Difference of means (B - A)	$t_{A:B}$	n	s	x̄	x̄	s	n
Jan.	+ 1.720	1.4700	56	4.384	62.325	64.045	5.283	22
Feb.	+ 0.989	0.8966	57	4.387	64.856	65.845	4.412	22
March	+ 0.059	0.0641	57	3.657	71.023	71.082	3.689	22
April	+ 0.510	0.9942	57	2.136	76.726	77.236	1.776	22
May	+ 1.489	3.6326**	57	1.577	82.856	84.345	1.775	22
June	+ 1.857	4.0484**	57	1.931	88.016	89.873	1.517	22
July	+ 1.120	3.0890**	57	1.501	89.335	90.455	1.283	22
Aug.	+ 1.422	3.6935**	57	1.565	89.259	90.681	1.447	22
Sept.	+ 0.682	1.3003	57	2.116	86.054	86.736	2.015	22
Oct.	+ 2.037	3.3481**	57	2.455	78.181	80.218	2.338	22
Nov.	- 0.052	0.0687	57	3.030	69.747	69.695	2.978	22
Dec.	+ 1.848	2.0591*	57	3.587	63.079	64.927	3.545	22

* Significant at .05 level ** Significant at .01 level

TABLE VI

Galveston

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" t test.

			A			B		
			Beginning of record through 1930			1931 - 1952 (both inclusive)		
Month	Difference of means (B - A)	t A:B	n	s	$\bar{x}$	$\bar{x}$	s	n
Jan.	+ 1.130	1.1381	56	3.903	59.261	60.391	4.057	22
Feb.	+ 0.875	0.9015	56	4.024	61.675	62.550	3.383	22
March	- 0.643	0.8318	56	3.113	67.452	66.809	2.962	22
April	- 0.852	1.6306	56	2.138	73.729	72.877	1.905	22
May	+ 0.050	0.1090	57	1.936	80.000	80.050	1.502	22
June	+ 0.089	0.1886	57	2.125	85.702	85.791	0.953	22
July	- 0.232	0.5851	57	1.805	87.832	87.600	0.680	22
Aug.	+ 0.084	0.2589	57	1.406	87.875	87.959	0.927	22
Sept.	- 0.108	0.2725	57	1.594	84.681	84.573	1.541	22
Oct.	+ 0.972	1.9417	57	2.008	77.637	78.609	1.958	22
Nov.	+ 0.135	0.1833	57	2.979	68.510	68.645	2.808	22
Dec.	+ 1.108	1.4301	57	3.186	61.774	62.882	2.806	22

TABLE VII

Brownsville

Comparison of mean monthly maximum air temperatures (°F.) for periods from beginning of record through 1930 (period A), and 1931 through 1952 (period B) by "student" t test.

			A			B		
			Beginning of record through 1930			1931 - 1952 (both inclusive)		
Month	Difference of means (B - A)	t A:B	n	s	$\bar{x}$	$\bar{x}$	s	n
Jan.	- 0.375	0.3377	46	4.418	69.261	68.885	3.412	20
Feb.	- 0.087	0.9583	46	3.392	72.357	72.270	3.382	20
March	- 1.358	1.4435	46	3.553	77.428	76.070	3.413	20
April	- 1.304	2.2045*	46	2.205	82.874	81.570	2.216	20
May	- 0.526	0.9960	46	1.965	86.926	86.400	1.985	20
June	- 1.334	1.9727	46	2.454	90.839	89.505	2.683	20
July	- 0.368	0.7707	46	1.797	92.058	91.690	2.407	20
Aug.	- 1.175	2.0581*	46	2.346	93.120	91.945	1.507	20
Sept.	- 0.700	1.1084	46	2.591	89.730	89.030	1.679	20
Oct.	+ 0.205	0.3109	45	2.544	84.560	84.765	2.230	20
Nov.	+ 0.094	0.1040	46	3.824	76.711	76.805	2.795	20
Dec.	+ 0.931	0.8879	46	4.147	70.659	71.590	3.298	20

* Significant at .05 level

with the 25° C. temperature level. The arrows in the figure indicate where the water temperatures cross the 25° level in the spring and in the fall. These anticipate the maximum air temperatures by a few days, but the average maximum air temperature is still a good guide for classifying the temperature environment of the oyster in the shallow estuarial waters of the Gulf Coast.

Discussion

Evidence has been presented from several sources supporting the view that there is a point between 20 and 25 degrees centigrade above which conditions become unfavorable for the survival of the individual oyster. Stauber (1950) suggests the possibility of physiological species on the basis of minimal temperatures necessary for spawning, and it is suggested, on the basis of Hopkins' (1931) work, that the minimal spawning temperature for the Gulf Coast might be 25° C. It is possible to conclude, from the point of view of mortality studies alone, that spawning weakens the oyster to the point of death, and that the mortalities mentioned here resulted solely from spawning. This theory cannot easily be reconciled with the fact that pumping rates are also reduced by the advance of temperatures above 25° C. It would seem that the oyster should filter as much water as possible following spawning in order to reestablish its energy reserves.

It is possible that within the physiological optimum temperature range of the species (15° to 25° C.) there could be races defined according to the critical temperature thresholds for spawning. These have been reported as 16.4°, 20° and 25° C. (Stauber, loc. cit.). If this is so, and the optimum physiological range is 15° to 25° C., then the upper limit of this range coincides with the highest of the critical spawning temperatures. This means that spawning in water whose temperatures run over 25° C. exhausts the energy reserves of the oyster at a time when conditions are not favorable for recovery. Accordingly, the oysters will be favored or disfavored as the temperature fluctuates below and above the 25° C. level.

Another factor which must be considered insofar as the mortality picture is concerned is the attack of the oyster by various disease organisms and predators. If the oyster is forced to spend much of the time closed because of unfavorable chemical and physical environmental elements, particularly at temperatures above 25° C., then it uses its energy reserves very rapidly and becomes easy prey to the predators, and especially to Dermocystidium marinum, which is evidently endemic in the waters, and is always in position to attack from the inside of the organism (Mackin, Owen and Collier, 1950). This situation is made worse by spawning.

At this point it is clear that when water temperatures persist for prolonged periods above 25° C. the oyster is at a disadvantage in pumping, cannot recover from the exhaustion of spawning, and is open to attack by a pathogenic fungus and by predators. The temperature in itself is probably not the lethal agent, but serves to bring the oyster within reach of these enemies.

Since the oyster does pump at high temperatures when the "carbohydrate" concentration of the sea water is sufficient, one would expect that there should be times and places when temperatures above 25° C. might be tolerated with fair success. This is exactly what we find, but unfortunately, we do not yet know enough about these natural carbohydrates to define the environmental conditions required for their maximum production.

EFFECTS OF TEMPERATURE ON THE DISTRIBUTION OF CRASSOSTREA VIRGINICA IN SPACE AND TIME

In the preceding section we have established through physiological experiments and field observations that, at least on some points along the Gulf of Mexico, oysters do not do well when the water temperatures exceed 25° C. It should be profitable, then, to examine the seasonal fluctuations in water and air temperatures, and to review the climate of the northern Gulf of Mexico insofar as that is possible.

Since information on water temperatures is not as generally available, and the records are not of as long standing as those for air temperatures, we are forced to derive water temperatures from those of the air in order to survey the past. In comparing air and water temperatures for the estuaries the Gulf Coast it is difficult to generalize. Water temperatures follow air temperatures closely when the body of water is comparatively shallow or presents a high surface-to-volume ratio. However, a great deal will depend on whether or not a given estuary receives a significant quantity of marsh drainage. This is particularly so in the summer months when the marshes are all exposed by low water during the day to a large amount of heat. Because of the black and gray mucks, the absorption of this heat is increased by the black-body effect. At night, when the marshes are covered by a relatively thin film of water, the temperature of the water will be raised by absorption of heat from the marsh muds, and then when it runs off with the ebb tide during the next day it will be exposed to additional radiation from the sun. Consequently, water temperatures in these shallow bays can run considerably higher than even the maximum air temperatures. Collier and Hedgpeth (1950, Fig. 6, p. 141) showed that the water temperatures of Copano Bay, Aransas Bay and the Gulf of Mexico at Port Aransas, ran 3° and 4° higher than the average monthly air temperatures at Corpus Christi. This difference was quite consistent from April through September, but as would be expected, is a little more erratic during the winter months.

From the point of view of oyster biology it would be more useful to accept the temperature fluctuations of the estuarial waters as approximating the maximum air temperatures rather than the means.

Brownsville, Galveston, New Orleans, Mobile, Pensacola and Tampa were selected as land stations with sufficient length of record to permit a valid examination of air temperature trends for the northern shores of the Gulf of Mexico. This comparison is between the mean monthly maximum air temperatures for the period 1931 to 1952 (both inclusive) and the period 1930 back to beginning of record. All pertinent data are tabulated in Tables II through VII, and the differences in the means are plotted in Figure 5.

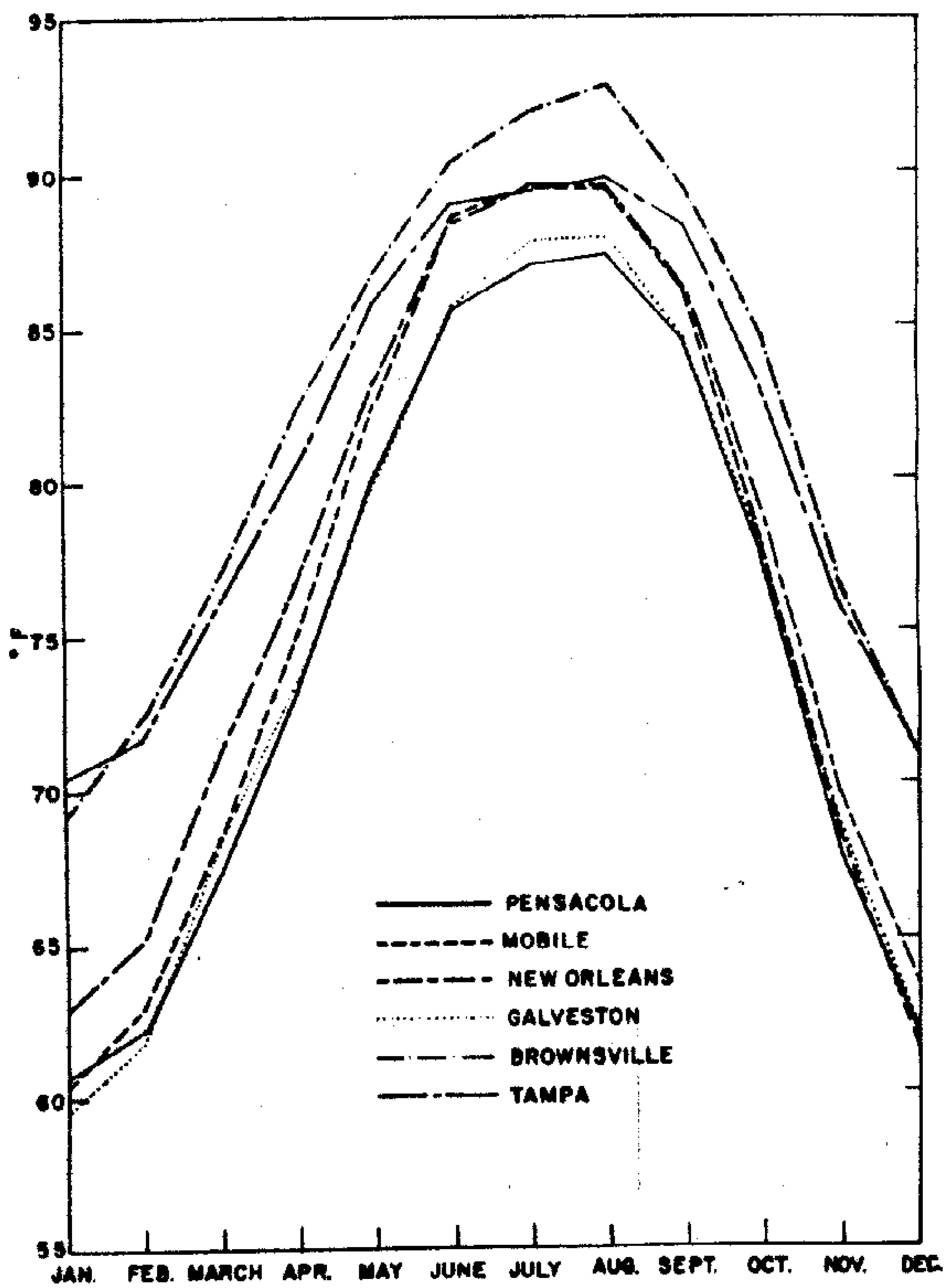

Figure 6. Mean monthly maximum air temperatures for all years of record for certain Gulf of Mexico points.

about 100 years ago and has accelerated in pace during the last thirty ye years or so." Again, quoting this time from Flint (1947): "Kinser demonstrated that mean annual temperatures have been rising at a rate falling between and 2.2° C. per century. The increase is evident not only in the norther hemisphere, but in the southern as well."

Collier and Hedgpeth (loc. cit.) point out some general similarities IN the Galveston area of the Gulf of Mexico to the Beaufort region of the mi Atlantic Coast. Ekman (1953) considers the coastal waters of Texas as tr pical in the summer and warm temperate in the winter with a corresponding f distribution. He also mentions Crassostrea virginica as being found [redacted] Further south, but says that it occurs as a community dominant only along the [redacted] northern coast of the Gulf of Mexico and along the eastern seaboard north of Flori da

In Figure 6 we have plotted the mean monthly maximum air temperature for certain points around the coast of the Gulf of Mexico. It will be [redacted] noted that Tampa and Brownsville have consistently higher maxima throughout the year with the exception that the summer maxima for Tampa are about the same as those of Mobile and New Orleans. With 25° C. (77° F.) as the maximum of The optimum range for Crassostrea virginica, this picture of seasonal maxima is consistent with Ekman's remarks concerning the distribution of this species in the Gulf of Mexico.

It is also to be observed that in the north Gulf (represented by [redacted] Pensicola, Mobile, Galveston and New Orleans) there are five months of favorable temperature levels, while in the south Gulf there are only three months. These periods are subject to some variation from year to year as can be se in Figures 7 and 8.

For the northern Gulf of Mexico, Pensacola, Mobile, New Orleans and Galveston have been selected as sample points. For all of these points, [redacted] records go back to at least 1880. The average monthly maxima for these points has been plotted for each year of record in Figures 7 and 8. What we consider be the optimum temperature range of the oyster, 53° to 77° F., has been indi cated for each month by cross hatching. We note that it is only during the months of November, December, January, February and March that the temperature ranges are comfortably within these limits. In April and October, the range is on the upper border, and in these cases it is clear that there will be some years in which April and October will be favorable to oysters, and many years when conditions during these months will not be favorable. It will be particularly noticed that for October conditions have been becoming increasingly unfavorable since about 1916.

Crassostrea virginica was established in the Gulf of Mexico in or near the Pliocene period (Dall, 1889), and at this time air and water temperature were lower than they are now. Phleger (1951) reported on a comprehensive study of the distribution of the Foraminifera in the Gulf of Mexico and the following interesting paragraph is quoted from his paper: "A cool water fauna is found in the lower part of most cores. This was deposited when surface water temperatures were lower than present surface temperatures in

TABLE VIII

Comparison of deviations (in month-degrees, F.) during the month of October, from 77° F. (25° C.) for the two 35 year periods, 1882-1916 (both inclusive), and 1917-1951 (both inclusive) at each of the four sample stations on the north coast of the Gulf of Mexico.

	1882-1916	1917-1951
Pensacola	+ 6.9	+ 24.5
Mobile	+ 18.8	+ 79.1
New Orleans	+ 34.0	+ 109.6
Galveston	+ 14.3	+ 51.9